

REPRODUCTIVE BIOLOGY AND POPULATION STRUCTURE OF THE
FIDDLER CRAB *UCA SUBCYLINDRICA* (STIMPSON)

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ABSTRACT

Comparatively large ova, low fecundity and low per capita egg production are adaptations to terrestrial habits in *Uca subcylindrica*. An unusual morphology of the genitalia appears to have co-evolved with the necessity for a lecithotrophic egg. Isolated populations are apparently sustained by rapid larval development. The crab stage population has a bimodal size-frequency distribution with an intermediate sex ratio pattern. Initially the sexes are equal, but males are more common in the larger size classes. Survival into the crab stage is relatively low. There is an increased rate of mortality with size. Only 30% of the individuals grow to modal carapace size; even fewer appear to participate in reproduction.

INTRODUCTION

Within *Uca*, the cosmopolitan genus of fiddler crabs, *Uca subcylindrica* (Stimpson) occupies a limited geographic range that coincides with the semi-arid zone near the mouth of the Rio Grande in the western Gulf of Mexico. Details of the species' biogeography and microhabitat ecology have been described by Thurman (1984). This species is extremely terrestrial in comparison to other members of the genus. Other than taxonomic treatments (Barnwell and Thurman, 1984), few observations of the crab's natural history are available. Fisk (1941) and Peyton *et al.* (1964) reported the occurrence of mosquito larvae in the burrows of *U. subcylindrica*. Preliminary observations of larval development were made by Thurman (1979) and extended by Rabalais and Cameron (1983). The present paper describes the reproductive biology and the consequence of anomalously rapid larval development on population characteristics of *U. subcylindrica*. Portions of this paper have appeared in abstract form (Thurman and Thurman, 1981).

MATERIALS AND METHODS

Uca subcylindrica were collected from 45 localities in south Texas and northeastern Mexico between 1972 and 1977 (Thurman, 1984). Six-hundred thirty-six (636) living specimens of this species were preserved in 70% ethanol. In addition, specimens of all other egg-laden fiddler crabs were collected. Egg diameter was estimated with the ocular micrometer of a stereo microscope by placing 1.0 mm-grid graph paper under a petri dish containing either fresh or preserved ova. Clutch sizes were calculated by counting the number of ova attached to a single pleopod of an egg-bearing female. This number was multiplied by the number of pleopods to obtain eggs per female (Gray, 1942). Larvae were reared from eggs in closed 4-liter plastic boxes containing 15‰ sea water as previously described (Thurman, 1979). Body length was measured in crab-stage individuals as the dorsal distance between the anterior and posterior

margins of the carapace. Carapace width was measured as maximum distance between the anterolateral margins.

Standard deviations are given with means. Unless otherwise stated, significance was determined by Student's *t*-Test or Chi-square Test.

RESULTS

Egg size (1.0 ± 0.01 mm diameter) and the number of eggs in relation to female size (Table I, Fig. 1) compare closely to that reported by Rabalias and Cameron (1983). The authors reported a linear relationship between female carapace width (x) and the number of eggs (y) carried ($y = 81.77x - 914.99$; $r^2 = 0.80$).

Five ovigerous female *Uca subcylindrica* were captured accounting for only 1.5% of all mature females in the collection (Table I). *U. subcylindrica* were not collected in October, November, June, or July, however reproduction probably does not occur during these months. This is indicated by two observations. First, no ovigerous females were found in collections made between December and March. Second, in this area it rarely rains between June and early August and most surface waters become hypersaline and ultimately evaporate (Behrens, 1966; Thurman, 1984). Thus, eggs are probably produced only during the spring and late summer rainy periods. The low frequency of ovigerous females in the collection suggests they are rare in the population, even during breeding periods.

Other species of *Uca* were found to produce eggs between February and September. The microhabitat ecology of each species has been described elsewhere (Thurman, 1982, 1984). The egg diameters of all species except *U. subcylindrica* were similar (0.25 ± 0.02 mm). The earliest reproducing species was *Uca spinicarpa* Rathbun, which was collected with eggs in February. Ovigerous *Uca panacea* Novak and Salmon, *U. rapax* (Smith), and *U. longisignalis* Salmon and Atsoides were not captured until March. For all species except *U. subcylindrica*, ovigerous females were collected throughout the summer months, but the greatest frequency of egg-laden females per sampling occurred in late August and September. During summer peaks in reproduction, at least 20 to 30% of any population sample contained ovigerous females. Only 10% of the *U. spinicarpa* were collected in "berry." The apparently low frequency of berried-females in *U. subcylindrica* contrasts sharply with these brackish and fresh water species. A larger number of eggs is produced by those species living near brackish habitats.

TABLE I

Egg production in Uca subcylindrica (Stimpson)

Carapace width (mm)	No. ova	Collection date
16.3	50	30 April
18.4	500	15 April
20.6	960	15 August
22.9	1000	28 August
*23.3	—	25 May

* From the museum collection of the University of Texas Marine Science Institute at Port Aransas. This specimen, labeled as *Uca pugnax*, was collected from the Aransas Wildlife Refuge by J. W. Hedgpeth in 1946.

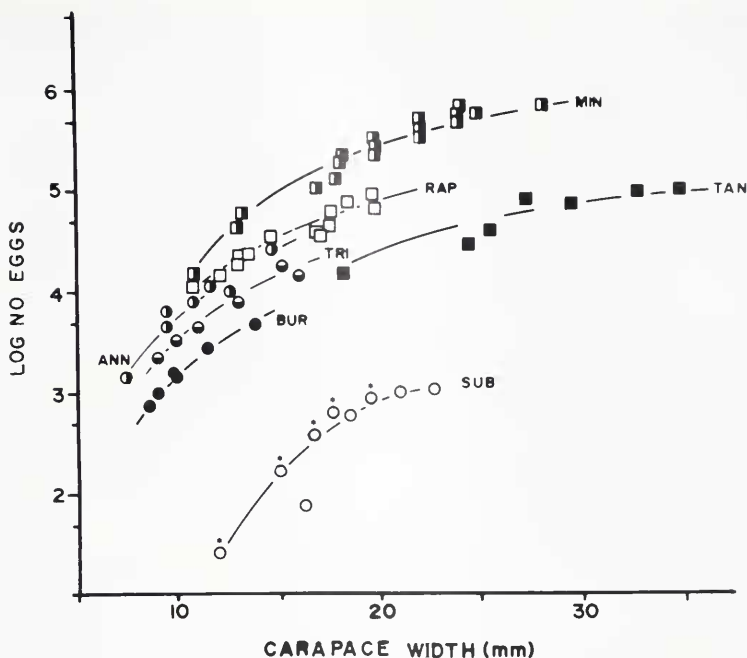


FIGURE 1. Variation in ova production by different species of *Uca*. Abbreviations: SUB = *U. subcylindrica*, $n = 46$ (○), BUR = *U. burgersi*, $n = 6$ (■), TRI = *U. triangularis*, $n = 5$ (●), ANN = *U. annulipes*, $n = 7$ (●), RAP = *U. rapax*, $n = 25$ (□), TAN = *U. tangeri*, $n = 7$ (■), MIN = *U. minax*, $n = 52$ (■). -*- indicates average for 1 mm width intervals from Rabalais and Cameron (1983).

In addition to season of egg deposition, the number of ova produced in each brood or clutch is of interest. Egg size is independent of female size. General brood characteristics have been reported for other Texas *Uca* (Rabalais and Cameron, 1983). The ova and clutch dimensions of *U. subcylindrica* are compared to allopatric congeners in Table II. The variation in number of eggs produced by different size classes in these species is shown in Figure 1. The data for *U. subcylindrica* are a combination of the counts in Table I and those provided by Rabalais and Cameron (1983). Ninety-five percent of egg production occurs by individuals with carapace lengths greater than 9.5 mm. In all species, as the size of the ovigerous female increases the number of ova carried per clutch becomes larger. However, there is considerable variation between species with respect to the maximum number of eggs carried by a female.

The distinctive structure of the male gonopodium and female gonopore found in *U. subcylindrica* is shown in Figure 2. Since the reproductive structure of other Gulf *Uca* have been published elsewhere, only a comparison with *Uca spinicarpa* is made here. Both male and female structures are much larger in *U. subcylindrica* than other species of *Uca*. The tip of the gonopod is about three times as broad while the aperture and genital operculum of the gonopore are seven to eight times larger in *U. subcylindrica* than those of other fiddler crab species. In the present examples, there are obvious physical restrictions associated with intraspecific reproductive compatibility.

The lecithotrophic egg in *U. subcylindrica* gives rise to rapidly developing larval stages. Larval development in most fiddler crab species lasts between two weeks and one month (Hyman, 1920; Herrnkind, 1968; Feest, 1969; Terada, 1979). Zoéal stages in *U. subcylindrica* last no longer than three days in culture (Thurman, 1979; Rabalais

TABLE II

Ova and clutch characteristic of Uca from different habitats

Species/reference	Habitat	\bar{X} Female carapace width (mm)	\bar{X} Ova radius (mm)	\bar{X} Egg volume (mm ³)	\bar{X} No. eggs brood	\bar{X} Clutch volume (mm ³)
<i>U. subcylindrica</i>	Tr	13.4	0.5	0.52	627	327.3
<i>U. burgersi</i> (Gibbs, 1974)	ST	10.4	0.18	0.024	1782	42.8
<i>U. triangularis</i> (Feest, 1969)	IT	9.6	0.12	0.007	3990	27.9
<i>U. annulipes</i> (Feest, 1969)	IT-B	11.3	0.12	0.007	6400	44.8
<i>U. rapax</i> (Greenspan, 1980)	IT-B	15.8	0.13	0.009	28500	256.5
<i>U. tangeri</i> (Feest, 1969)	B-R	27.4	0.12	0.007	59000	413.0
<i>U. minax</i> (Gray, 1942)	R	20.3	0.13	0.009	184928	1666.3

Tr = terrestrial, ST = semiterrestrial, IT = intertidal, B = brackish, R = riverine.

and Cameron, 1983). There may be two or three instars before the megalopae appear. The megalopae metamorphose to the first crab stage within seven to ten days after hatching from the ova. The zoea do not feed. Megalopae, however, accepted brine shrimp. Some were observed to be cannibalistic.

Basic morphometric data were taken from crab-stages of the fiddler crabs. Carapace length and width in *U. subcylindrica* are closely correlated (Fig. 3). On a population basis, *Uca subcylindrica* appears to have the smallest average carapace length of all fiddler crab species in the region (Table III). Using carapace length, the size distribution of *U. subcylindrica* is illustrated in Figure 4. Over the sample, average carapace length is 8.1 ± 0.6 mm. However, the size-frequency distribution does not fit a single normal distribution ($P < 0.05$) by Chi-square test. Rather, these data are better described as a bimodal distribution. Subpopulation I possesses individuals with carapace lengths less than 8.5 mm ($\bar{X} = 5.9 \pm 0.6$ mm). Larger individuals form subpopulation II ($\bar{X} = 10.4 \pm 0.8$ mm). Each subpopulation fits a Poisson frequency distribution ($P > 0.05$; Sub_I $\chi^2 = 13.84$; Sub_{II} $\chi^2 = 12.08$). Within each there is no significant difference between mean carapace length in males and females. Individuals forming subpopulation I were segregated into discrete samples for each month between December and March. There are slight but insignificant differences in mean-monthly carapace length. Carapace length in subpopulation I increased by 1.0 mm between January and March. The carapace lengths of other species of *Uca* were unimodally distributed.

Across the entire population, two allometric abdomen forms are seen that are associated with puberty in female crustacea (Huxley, 1924; Hartnoll, 1974; Haley, 1969, 1973). Regardless of size, individuals having one enlarged cheliped, gonopodia, and a narrow abdomen were considered to be males. In the remainder of the population, individuals with two small chelipeds and sternal gonopores were considered females regardless of abdomen width. Some females have very broad while others possess narrow abdomens. In the lower portion of Figure 4, females with equal chelipeds but less than 5.5 mm carapace length all have narrow abdomens. The frequency of broadness increases as the carapace length reaches 8.0 mm. In larger size categories, all

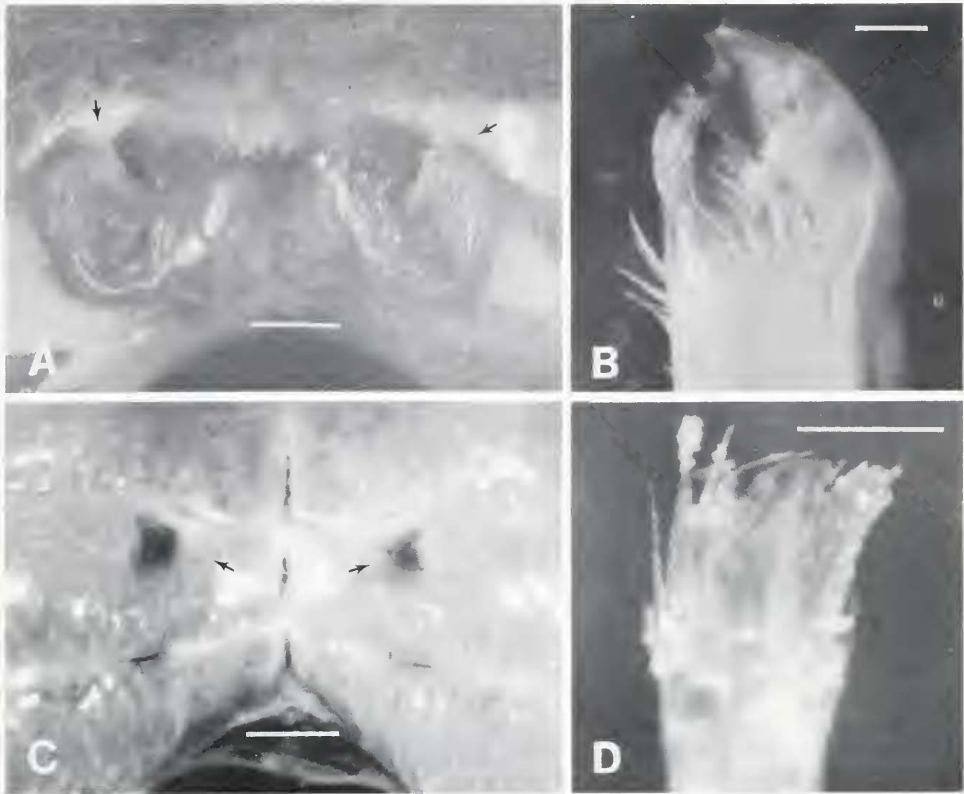


FIGURE 2. Morphology of the external reproductive structures found in Gulf *Celuca*. A. Gonopores of female *Uca subcylindrica*. Bar = 1.0 mm, arrows indicate genital tubercle. B. Posterior perspective of right gonopodium from male *U. subcylindrica*. Bar = 0.5 mm. C. Gonopores of female *Uca spinicarpa*. Bar = 1.0 mm, arrows indicates lateral margins. D. Lateral perspective of right gonopodium from male *U. spinicarpa*. Bar = 0.5 mm. Examples taken from individuals with carapace width between 17.0 and 18.0 mm.

females possess broad abdomens. The size intervals between 5.5 and 8.0 mm within subpopulation I represent a transitional phase to sexual maturity. This interval appears to represent morphologically but not functionally mature females since egg production is not observed until the crabs are in the 9–10 mm size category (Fig. 4).

Based on cheliped asymmetry and abdomen structure, the probability of maleness (P_m) averages 0.58 ± 0.10 (58%) over the entire population. In subpopulation I, the prepuberty sample, $P_m = 53 \pm 3\%$. This increases to $61 \pm 4\%$ in subpopulation II. P_m is calculated for each 1.0 mm length interval and compared throughout the population in Figure 5. Since the relative number of males increases with size, the sex ratio in the population is considered to be “intermediate” as described by Wenner (1972). A significant correlation coefficient of 0.727 is seen for the nine categories of carapace length ($P < 0.005$). The male:female ratio is between 1.8 and 2.3 in size classes greater than 8.0 mm. Since differential migration patterns between the sexes appears to be negligible in this habitat (Thurman, 1984), these data suggest that females either succumb to environmental pressures earlier or grow less rapidly than males after puberty as proposed by Fielding and Haley (1976) for other crabs. However, Colby and Fonseca (1984) have found reproductively active female *U. pugilator* to grow slower than males.

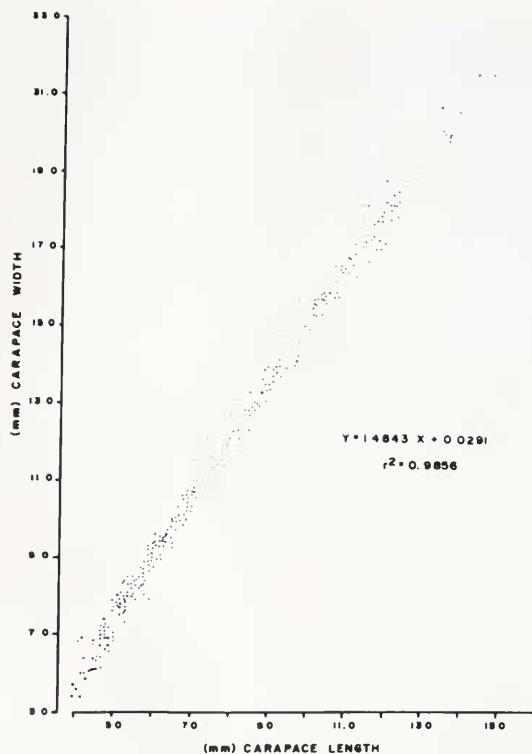


FIGURE 3. Relation between carapace length and width in *Uca subcylindrica* ($n = 417$). Linear regression calculated by least squares method for $n = 150$.

Survivorship curves can be used to compare the degree of adaptive success among species (Ricklefs, 1973). Assuming that size distribution represent losses from each morphological cohort due to death and/or growth, the logarithm of percent survival can be related to carapace size in four species of *Uca* that differ in microhabitat ecology

TABLE III

Relation between carapace length and width in *Uca* from the western Gulf of Mexico

Subgenus/ species	n	Carapace		y = mx + b	r ²
		length (\bar{X}) (mm)	Width (\bar{Y}) (mm)		
<i>Celuca</i>					
<i>subcylindrica</i>	150	8.8 ± 2.9	13.4 ± 4.4	1.4843x + 0.0291	.9856
<i>spincarpa</i>	156	10.5 ± 2.9	14.6 ± 3.1	1.4944x - 0.0263	.9768
<i>panacea</i>	125	10.0 ± 2.5	15.5 ± 3.5	1.4290x - 0.0191	.9879
<i>Mimuca</i>					
<i>rapax</i>	123	10.5 ± 2.2	15.9 ± 3.4	1.5464x - 0.0315	.9789
<i>longisignalis</i>	74	11.5 ± 2.7	17.0 ± 4.0	1.4993x - 0.0283	.9851
<i>vocator</i>	19	9.7 ± 2.7	13.3 ± 4.1	1.5190x - 0.1416	.9952

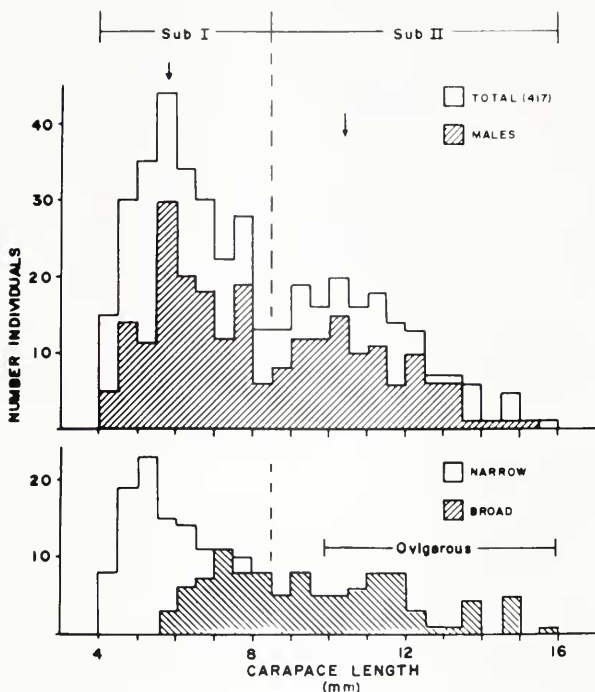


FIGURE 4. Size-frequency distribution of *Uca subcylindrica*. Upper graph: total/male component. Lower graph: female component. Sub I = subpopulation I, Sub II = subpopulation II. Arrows indicate mean carapace lengths for each subpopulation (5.9 ± 0.6 , 10.4 ± 0.8 mm, respectively). Ovigerous size intervals indicated by bar in lower graph.

(Fig. 6). Since each grows to a different maximum size, absolute body length has been converted to a percent maximum size. The data for *U. burgersi* is taken from Gibbs (1974), *U. pugnax* from Huxley (1924), and *U. panacea* from Powers (1975). The patterns of survival can be identified among the basic schemes of Deevey (1947). They appear to be either type I where mortality is low except in larger size classes or type II in which mortality increases at a constant rate with size. A constant mortality rate is expressed as the linear-exponential line. Species that live in more mesic habitats, such as *U. pugnax* and *U. panacea*, have type I survivorship. More terrestrial species like *U. burgersi* and *U. subcylindrica* have type II curves. The *U. subcylindrica* curve is closer to being exponential than *U. burgersi*. Comparisons between species can be made by determining what portion of the populations achieve modal size categories. About 80% of *U. pugnax* and *U. panacea* survive to the modal-length interval. On the other hand, only 48% of the *U. burgersi* and 30% of the *U. subcylindrica* attain the same relative size. Mortality in the smaller size categories is greater in the terrestrial species.

DISCUSSION

Crustaceans have adapted to terrestrial habitats through various morphological, physiological, and behavioral mechanisms. Supralittoral and terrestrial life for brachyurans has been complicated by two major problems: (1) continuance of reproduction and development and (2) regulation of temperature, salts, and water (Bliss, 1968).

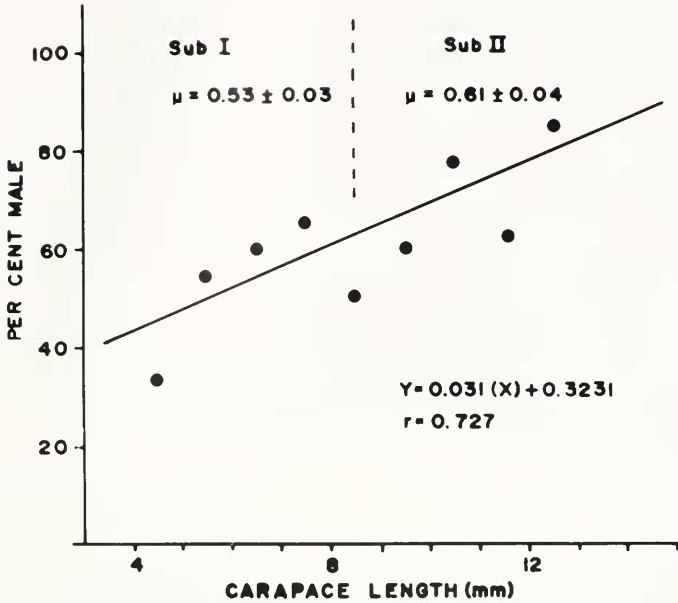


FIGURE 5. Percent males (P_m) *U. subcylindrica* in each 1.0 mm carapace length size interval. Linear regression computed by least squares method. Mean P_m for each subpopulation indicated.

Previously, Crane (1975) regarded the Red Sea as the most saline body of water inhabited by fiddler crabs. She reported the presences of three widely distributed Indo-Pacific species in habitats with salinities typically between 37 and 40‰. The *Celuca* appear to be the most successful of all subgenera in adapting to terrestrial habitats. From this terrestrial vantage point, *Uca subcylindrica* are unique among the fiddler crabs. Their limited geographic range is coincident with isolated lagoons in semi-arid south Texas and northeastern Mexico with salinities occasionally over 100‰ (Thurman, 1984). This species occupies very deep burrows near ephemeral bodies of water characterized by wide fluctuations in salinity up to 70‰ (*cf.* Hedgpeth, 1953). A continued survival of the species in this harsh habitat requires special modifications in reproduction. The reproductive biology of *Uca subcylindrica* contains anomalous features when compared to other species of fiddler crabs. Adaptations in egg production and larval development are ultimately reflected in the population structure of the species.

Early development

The terrestrial ecology of *U. burgersi* has been documented by von Hagen (1970b) and Gibbs (1974). This species is commonly found in habitats with salinities between 3.3 and 60.0‰, possesses extraordinary osmoregulatory abilities (Schmidt-Neilsen *et al.*, 1968), and has large eggs (0.36 mm dia.). The low ratio of ovigerous females observed in the present population sample (0.78%) is similar to the 6 females found by Gibbs (1974) in a sample of 535 *Uca burgersi* Holthuis. This statistic was estimated by a thorough transect and field study involving 45 crab populations in south Texas and Mexico (Thurman, 1984). The sampling of Rabalais and Cameron (1983) was systematically biased for ovigerous *U. subcylindrica* ($n = 41$) and could not be con-

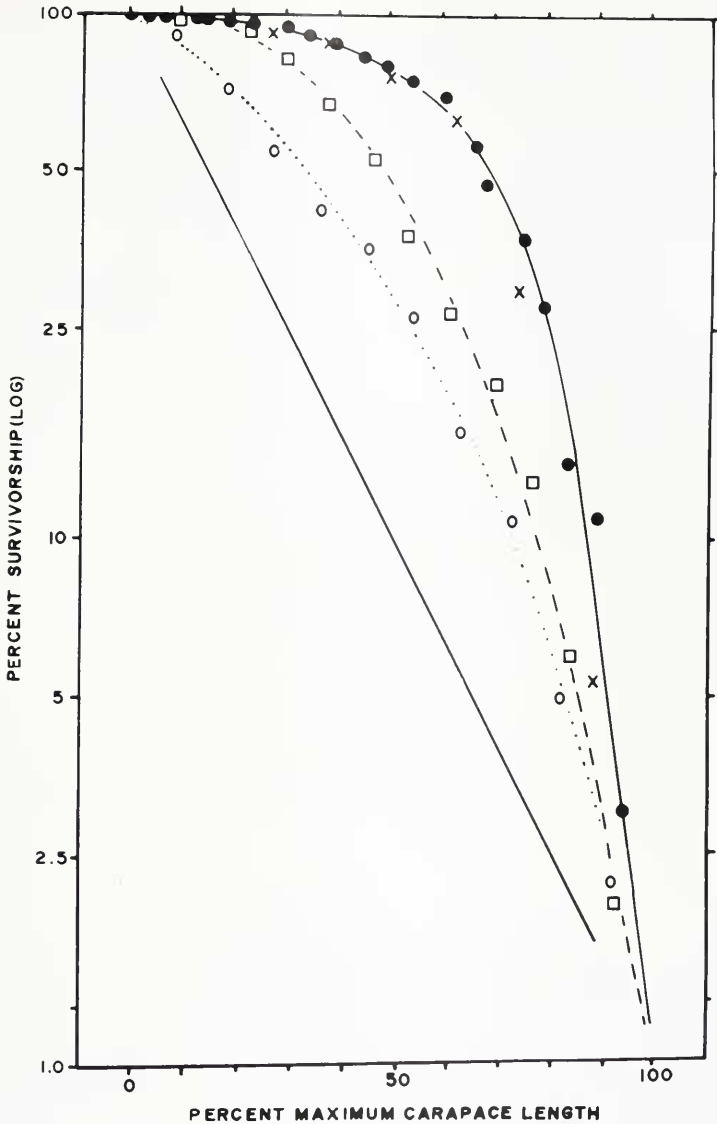


FIGURE 6. Survivorship curve adapted from Figure 4. *Uca subcylindrica* (O), *Uca pugnax* (●), *Uca panacea* (X), and *Uca burgersi* (□). All percents calculated for minimum to maximum size interval within each species. Linear line = constant exponential rate of decrease.

sidered in population estimates of reproductive potential. On Trinidad, the percent female *U. burgersi* with mature spermatheca is the lowest among nine species of fiddler crabs. Per capita frequency of reproduction is inversely correlated with terrestriality. Since *U. subcylindrica* is even more terrestrial than *U. burgersi* (Thurman, in press), it is not surprising that similar reproductive capabilities have evolved. The low fecundity and frequency of egg-production as well as large ova are parallel adaptations in the two ecologically similar species (Table II).

Early development in benthic marine invertebrates may vary along a spectrum from plankto- to lecithotrophy. Whatever the pattern, it represents the most energetically efficient strategy in producing the largest number of individuals surviving to produce eggs (Vance, 1973). When closely related species are compared, there is a fairly constant correspondence between egg size, developmental pattern, and size at metamorphosis (Christiansen and Fenchel, 1979). These characteristics appear to converge. The necessity for lecithotrophism will depend upon several abiotic factors. Generally, low food availability and temperatures are responsible for lecithotrophy in benthic polar and abyssal communities. However, as Thorson (1950) pointed out, at lower latitudes where predictable but short periods of rainfall occur, lecithotrophic development may occur in organisms with reproductive periods restricted to these seasons. Since reproductive periods in *U. subcylindrica* are synchronized with short rainy seasons, the latter strategy appears to be correlated with lecithotrophism in this subtropical species.

A broader perspective for fecundity in temperate and tropical *Uca* is outlined in Table II. Mean values for ovigerous female, ova, and clutch size are given for each species. The general habitat obtained from Crane (1975) for each is indicated along with an estimate of average ova and total clutch volume. Both size and number of eggs produced appear to correspond to environmental conditions. These are inversely related when intrageneric comparisons are made. Generally, riverine species possess the largest mean carapace width and carry the largest number of ova. On the other hand, the semi- and fully terrestrial species are smaller in body and clutch size. If one assumes the ova of each species are elementally similar, clutch volume may be an approximation of reproductive economics (Coe, 1949). For preliminary comparisons between species this is a reasonable measure since many details of the reproductive cycles for each species are not known. Although the eggs of *U. subcylindrica* are large (radius = 0.5 mm), clutch volume is well within the range of values calculated for other congeners. The apparent expense in producing an egg brood in the terrestrial species is no greater than that for female *U. rapax* or *U. tangeri* which carry a large number of smaller eggs. Consequently, there appears to be some certainty that a sufficient percentage of *U. subcylindrica* eggs will survive to reproduce as adults. To insure development, *U. subcylindrica* incubate their eggs for one to one-and-a-half months rather than 12 to 15 days as other *Uca* (Rabalais and Cameron, 1983).

As illustrated in Figure 2, the external genitalia of *U. subcylindrica* are large when compared to other *Uca*. Crane (1975) and Felder (1973) have used these as reliable taxonomic characters. However, these structures appear to possess little information on which to base any conclusions concerning phylogenetic affinity. Since survival in the semiarid habitats of this species has required the evolution of lecithotrophic embryos, the diameter of the gonopore has increased to allow oviposition of larger eggs. Since sperm transfer occurs by copulation in this genus, the large gonopod of the male has been selected to produce efficient intromission.

The abbreviated pattern of larval development in *Uca subcylindrica* provides two advantages in colonizing the semi-arid habitats with nontidal, ephemeral water found in south Texas (Thurman, 1984). First, larval success in settling depends upon the length of precompetent and competent periods, as well as predation rates. For invertebrates in general, the duration of each phase is correlated with the prevailing on-shore and off-shore currents experienced during planktonic stages of development (Jackson and Strathman, 1981). In other *Uca*, larval release and settling are synchronized with local tides to facilitate dispersal and protection from planktivores (Christy, 1978, 1982; Wheeler 1978). The upper Laguna Madre has no well-defined tide or

circulation pattern. Meteorological events are more effective in producing basin flushing than are predictable hydrographic forces (Smith, 1975). Since there is little prospect for oceanic dispersal of *U. subcylindrica* zoea, selection has minimized the duration of precompetent zoeal stages. Modifications such as this are known in the early life cycle of other crustacean species with limited dispersion potential. For example, the hymenosomatid crabs of western Australia assure recruitment into isolated populations by eliminating the megalopa stage of development. Rapid development in local nursery areas has evolved to compensate for low fecundity in these populations (Lucas, 1975).

This pattern is an advantage for a second reason. The length of time for zoeal phases is modified by diet and temperature. However, the duration of the megalopa stage is relatively constant in most *Uca* (Vernberg and Vernberg, 1975; Christiansen and Yang, 1976). In south Texas, brief periods of rain usually occur in May and September interrupting long periods of drought (Behrens, 1966). Since hypersalinity inhibits development (Rabalais and Cameron, 1982), egg deposition and rapid ontogeny in *U. subcylindrica* during wetter months is an optimal strategy capitalizing upon short but predictable fluctuations in an otherwise arid environment. Due to the compression of development time, the large, lecithotrophic larvae of this species do not require planktonic feeding. Consequently, non-planktonic development reduces predation mortality nearly to zero (Vance, 1973). Owing to the importance of osmotic stress over predation in this habitat, the anomalous development of this species compensates for both limited dispersal and physiological problems. If abiotic mortality factors are constant, rapid but isolated development ensures recruitment in an inhospitable habitat. In a discussion of tropical gastropods, Vermeij (1978) has suggested that marine species inhabiting lagoons and isolated inshore habitats tend to develop as endemic forms while more planktonic species are cosmopolitan. This observation appears to have some application in understanding the evolution of *U. subcylindrica* and the general level of fiddler crab endemism in the Gulf of Mexico (Barnwell and Thurman, 1984). This accelerated ontogeny has a pronounced effect on crab population size-structure.

Population structure

The structure and sex ratio in populations of *U. subcylindrica* can be compared to published data on more widely distributed crustaceans and fiddler crabs. The population structure of this species is more similar to crustaceans from higher latitudes than less terrestrial members of its own genus. The size-frequency distribution of a population is a dynamic characteristic that can change throughout the year as a result of reproduction and rapid recruitment from larvae. Several investigations have observed unimodal population size-structures in more slowly developing species of *Uca*. These include *U. pugilator* at Woods Hole (Huxley and Callow, 1933), *U. panacea* (Powers, 1975), and *U. pugnax* (Huxley, 1924) from the temperate zone where reproduction occurs with intensity between July and September. More southerly population of *U. pugilator* exhibit a progression in modal size-frequency distribution throughout the reproductive season (Colby and Fonseca, 1984). Tropical populations of *U. rapax*, *U. cumulanta* (Ahmed, 1976), and *U. burgersi* (Gibbs, 1974) are also unimodally distributed by size class. These species appear to reproduce more or less continuously throughout the year. On the other hand, the impact of recruitment from rapidly developing larvae has been reported in boreal crabs. The size frequency distribution of the crab stage in *Pisidia longicornis* is bimodal. Population recruitment occurs on an annual basis and development takes only three to four months (Samuelson 1970;

Smaldon 1972). The larger "adult" component is stable throughout the year. Smaller size categories correlate with larval settlement and growth processes throughout the year. In *U. subcylindrica*, body-size is bimodally distributed as a result of lecithotrophism and accelerated development. Growth of larvae into crabs in less than two weeks produces rapid seasonal recruitment into smaller size classes before ephemeral nursery grounds can evaporate.

Sex ratios have been reported for several species of fiddler crabs and appear to be related to the system of mating used by each (Christy and Salmon, 1984). Most exhibit the intermediate sex ratio pattern described by Wenner (1972). Powers (1975) found the percent males (P_m) to average 63% for *U. panacea* and 52% for *U. rapax* (= *U. virens*) in south Texas. *U. pugilator* in North Carolina has an average P_m of 39% (Colby and Fonseca, 1984). Along the temperate Atlantic coast, *U. pugnax* populations may vary in P_m from 53% in Georgia (Wolf *et al.*, 1975) to 59% in Massachusetts (Valiela *et al.*, 1974). This may be increased to 83% following an ecocatastrophe (Krebs and Burns, 1977). This species differs from others by having a P_m that decreases with size class. In tropical Venezuelan populations, the P_m of *U. rapax* is 59% while *U. cumulanta* is 54% (Ahmed, 1976). *Uca burgersi* populations on Barbuda have a P_m of 67% (Gibbs, 1984). The ratio of 58% males observed in *U. subcylindrica* is similar to the frequency observed in other *Uca* populations; the P_m increases with the size category just as in its tropical relatives.

Few females appear to survive into the larger size categories. Less than 25% of the entire population survives to size of first reproduction (9.5 mm body length). Although selection has reduced ontogeny and increased ova size, a delay in ova production to later in life can decrease the reproductive capacity of a species since mortality increases with size. However, all measurements of reproductive success are higher for individuals with a delayed onset of reproduction (Schall and Leverich, 1981). In fiddler crabs, larger individuals produce larger egg broods and apparently experience greater success in finding mates (Greenspan, 1980). In *U. subcylindrica* populations, rapid development and a delay in size of first reproduction may be balanced against the respective risks of mortality owing to abiotic factors. This overall reproductive strategy would assure a high return on reproductive investments and population recruitment in an inhospitable environment. This is accomplished without creating an excessive reproductive load with a large volume of unsuccessful offspring.

In conclusion, the single greatest stimulus to fiddler crab evolution is the presence of an unoccupied habitat (Crane, 1975). Specializations within the genus have led members to radiate in three directions: (a) into more terrestrial habitats, (b) to a greater partitioning of existing habitats between co-existing species, and (c) to increased sociality. Crane remarked that the unusually round body and striking reproductive appendages of *U. subcylindrica* are useful for its identification. In order to occupy more terrestrial habitats, the crab carapace has evolved as an arched, semi-cylindrical structure with increased volume. In addition, the more terrestrial representatives have broader frontal regions and short eyestalks and orbitals when compared to amphibious relatives (von Hagen, 1970a). Generally, less tomentose legs and carapace are found in more recently evolved terrestrial species (von Hagen, 1970b). The pubescence and long setae in *U. subcylindrica* appear to be adaptations for acquisition of substrate water in a dry environment as in other species (Thurman, 1982, 1984; Wolcott, 1984). Consequently, the tomentum in this species is a more highly evolved rather than a primitive characteristic. Maxillipeds, genital armature, acoustical signaling, combat behavior, and reproductive physiology are additional modifications associated with terrestrial adaptation (von Hagen, 1970c, 1975; Crane, 1975). Structure of the repro-

ductive apparatus reflects a selective response to large ova and mating in a semi-arid habitat. The body structures and reproductive armature reflect ecological adaptation rather than phylogenetic affinity.

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